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15 Paleobiology of Santacrucian caviomorph rodents: a morphofunctional approach

Adriana M. Candela, Luciano L. Rasia, and María E. Pérez

Abstract

Caviomorphs constitute a monophyletic group, representative of the oldest rodent radiation in South America. Since the Oligocene they have contributed importantly to the fossil communities of South American mammals. Today, caviomorphs display a diverse array of locomotor and feeding behaviors, occupying a wide range of habitats in which they consume a variety of food items. In this contribution, we analyze species of Santacrucian caviomorphs from a morphofunctional perspective in the context of extant caviomorph behavioral diversity, in order to evaluate their paleobiology and its paleoenvironmental significance. Body masses based on Santacrucian specimens were estimated by applying published equations. Reconstructions were made of areas of origin and insertion of the main masticatory muscles following the muscular pattern observed in living caviomorphs. On this basis, functional analyses of the masticatory apparatus were performed. Major postcranial features in extant caviomorphs identified as functionally associated with different locomotor habits were used as a model to evaluate the functional significance of the postcranial features in Santacrucian species. Santacrucian caviomorphs examined show the range of body mass from small- to relatively large-sized living caviomorphs. The porcupine *Steiromys duplicatus* and the dasyproctid *Neoreomys australis* present features that indicate a diet of harder and more abrasive food items than those consumed by living Neotropical phylogenetically related species. Features of the masticatory apparatus of the eocardiid *Eocardia fissa* are compatible with a wide feeding behavior, including abrasive food. *Steiromys duplicatus* was a semi-arboreal form, which did not achieve the degree of specialization that is seen in the Neotropical extant *Coendou*. *Eocardia fissa* was a cursorial agile rodent, similar to living *Pediolagus salinicola*. *Neoreomys australis* was a cursorial species, more similar to living *Agouti paca* than to *Dasyprocta* species. Santacrucian caviomorphs could have lived in an environment like the Cerrado biome, showing differential utilization of food resources and locomotor behaviors.

Resumen

Los caviomorfos constituyen un clado representativo de la más antigua radiación de roedores en América del Sur. Desde el Oligoceno fueron un importante componente de las comunidades de mamíferos fósiles de América del Sur. Actualmente los caviomorfos muestran una gran diversidad de comportamientos de locomoción y alimentación, ocupando diferentes hábitats en los cuales consumen variados tipos de alimentos. En esta contribución se analizan especies de caviomorfos Santacrucenses desde una perspectiva morfofuncional, en el contexto de la diversidad de comportamientos de caviomorfos vivientes, con el objeto de evaluar su paleobiología y significado paleoambiental. Las masas corporales de los especímenes analizados fueron estimadas aplicando ecuaciones publicadas. Las reconstrucciones de las áreas de origen e inserción de los principales músculos masticatorios fueron realizadas siguiendo el patrón observado en caviomorfos vivientes. Sobre esta base, se realizó el análisis funcional del aparato masticatorio en las especies fósiles examinadas. Los rasgos postcranianos funcionalmente asociados con diferentes hábitos locomotores en caviomorfos vivientes fueron usados como modelo para evaluar el significado funcional de los presentes en las especies extintas. Éstas muestran el rango de masa corporal comprendido entre las más pequeñas a las relativamente más grandes especies de caviomorfos vivientes. El puercoespín *Steiromys duplicatus* y el dasipróctido *Neoreomys australis* presentan rasgos que indican una dieta basada en alimentos más duros y abrasivos que aquellos consumidos por las especies neotropicales vivientes filogenéticamente relacionadas. Rasgos del aparato masticatorio del eocárdido *Eocardia fissa* son compatibles con un comportamiento alimenticio relativamente generalista, incluyendo alimentos abrasivos. *Steiromys duplicatus* habría sido una forma semi-arborícola que no alcanzó el grado de especialización observado en el género neotropical viviente *Coendou*. *Eocardia fissa* fue un roedor cursorial ágil, similar al cávido viviente *Pediolagus salinicola*. *Neoreomys australis* fue una especie cursorial más similar a la especie viviente *Agouti paca* que a *Dasyprocta* spp. Los caviomorfos Santacrucenses habrían habitado un ambiente similar al Bioma del Cerrado, mostrando diferentes patrones de utilización de recursos alimenticios y comportamientos de locomoción.

Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation, ed. Sergio F. Vizcaíno, Richard F. Kay and M. Susana Bargo. Published by Cambridge University Press. © Cambridge University Press 2012.

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15.1 Introduction

Caviomorphs constitute a very diverse and ancient monophyletic group of rodents (e.g. Huchon and Douzery, 2001; Churakov *et al*., 2010), endemic to Central and South America. Recorded since the Late Eocene? – Early Oligocene (Wyss *et al*., 1993; Frailey and Campbell, 2004; Vucetich *et al*., 2010), caviomorphs evolved in isolation during most of the Cenozoic, forming part of all of the fossil communities of South American mammals, particularly of those recorded in Patagonia. During their long evolutionary history they developed a significant taxonomical richness (e.g. McKenna and Bell, 1997; Vucetich *et al*., 1999). With about 59 genera and 250 extant species grouped in 12 families (Woods and Kilpatrick, 2005; Honeycutt *et al*., 2007), caviomorphs comprise a notable component of the faunas of living Neotropical mammals. They show a wide range of body size, from about 200 g, as in some echimyids, to 50–60 kg, as in the capybara. In terms of ecology and lifestyles, caviomorphs display a diverse array of locomotor behaviors and use of substrate, ranging from cursorial, saltatorial, semi-fossorial, and fossorial, to arboreal and swimming forms, occupying a wide range of habitats (e.g. Redford and Eisenberg, 1992; Elissamburu and Vizcaíno, 2004). Although basically herbivorous, living species consume varied food items, such as fruits, seeds, leaves, and grasses, and display diverse dietary preferences (e.g. Nowak, 1991; Redford and Eisenberg, 1992; Emmons and Feer, 1997). Among Santacrucian (late Early Miocene) mammals, caviomorphs are represented by numerous species (e.g. Ameghino, 1887; Scott, 1905; Candela, 2000; Kramarz, 2006; Pérez, 2010a), many of them known by well-preserved remains representing all the major clades recognized within this group, i.e. Cavioidea, Erethizontoidea, Chinchilloidea, and Octodontoidea (Fig. 15.1). Therefore, comparisons between Santacrucian and living caviomorphs can be made within the same phylogenetic levels. In spite of the important diversity and in many cases the exceptional preservation of the caviomorphs from the Santa Cruz Formation (late Early Miocene), inferences on their possible feeding habits and substrate preferences were based mainly on allied extant taxa (with some exceptions; see Candela and Vizcaíno, 2007; Candela and Picasso, 2008). Unlike other mammalian lineages (e.g. Vizcaíno *et al*., 2010), morphofunctional, ecomorphological, and biomechanical studies as a basis for understanding paleobiological aspects in Santacrucian caviomorphs are limited. Some species, such as those of the cavioid clade, represent the earliest caviomorphs with known postcranial remains. In this context, analyses of these remains will lead to an improved understanding of the early history of the locomotor behaviors in different lineages of Caviomorpha.

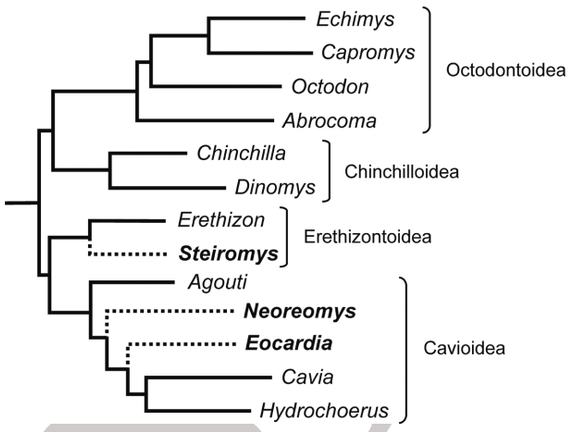

Fig. 15.1. Cladogram of Caviomorpha (taken from Blanga-Kanfi *et al*., 2009). For the phylogenetic position of *Eocardia* and *Neoreomys* we follow Pérez (2010b). Santacrucian genera in bold.

In this contribution we analyze exceptionally well-preserved osteological remains of species of Santacrucian caviomorphs belonging to Erethizontidae, Dasyproctidae, and "Eocardiidae" from a morphofunctional perspective, in order to expand our knowledge of their paleobiology. On this basis, we evaluate the paleoenvironmental significance of Santacrucian caviomorphs.

15.2 Santacrucian rodents in the context of Caviomorpha

Erethizontidae, the New World porcupines, are a distinctive clade of caviomorph rodents, known in South America since the Late Eocene–Late Oligocene (see Wood and Patterson, 1959; Candela, 2000; Frailey and Campbell, 2004). One characteristic that makes them easily recognizable among rodents is the presence of sharp quills. Living Neotropical porcupines represent one of the several radiations of mammals adapted to a strictly arboreal life and include approximately 15 species, extending from northern Uruguay and Argentina to southern Mexico (Emmons and Feer, 1997). They live mainly in different types of forests (e.g. rainforest, Atlantic forest, semi-deciduous forest, gallery forest; Emmons and Feer, 1997) of the Brazilian Subregion. With the exception of *Chaetomys subspinosus*, species of *Coendou* comprise the totality of Neotropical porcupines (Handley and Pine, 1992). Erethizontids are the only caviomorphs that survived in North America after their ingression during the Great American Biotic Interchange. The semi-arboreal *Erethizon dorsatum*, the only extant species in North America, is distributed from northern Mexico to Alaska and Canada. It lives principally in warm forests and tolerates some climatic seasonal variation

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(Roze, 1989). Fossil erethizontids were particularly abundant in Patagonia from the Late Oligocene to the Middle Miocene, during which they reached a considerable taxonomic diversity (e.g. Wood and Patterson, 1959; Candela, 1999, 2000, 2003; Kramarz, 2004). Santacrucian porcupines are grouped in the genus *Steiromys* Ameghino, 1887 (the most diverse of the extinct Erethizontidae and the first described by Ameghino as a member of this clade) which includes four (*S. duplicatus* Ameghino, 1887, *S. detentus* Ameghino, 1887, *S. principalis* Ameghino, 1901, *S. annectens* Ameghino, 1901) and possibly five (*S. intermedius* Scott, 1905; see Candela, 2000) species. *Steiromys duplicatus* is one of the most abundant Miocene porcupines from Patagonia.

In the extant Cavioidea, Dasyproctidae is represented by *Dasyprocta* (agoutis) with 11 species and *Myoprocta* (acouchis) with two species. All are extremely agile cursorial forms, inhabiting tropical and subtropical forested habitats and scrublands of the Brazilian Subregion (Nowak, 1991; Redford and Eisenberg, 1992). Dasyproctids are recognized since the Late Eocene? of Peru (Wyss *et al*., 1993; Flynn *et al*., 2003; Frailey and Campbell, 2004). Several genera from the Late Oligocene–Middle Miocene of Bolivia, Argentina, and Colombia have been assigned to this clade (e.g. Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Kramarz, 1998, 2006; Fields, 1957; Walton, 1997). However, the phylogenetic relationships of the extinct taxa with *Dasyprocta* and *Myoprocta* have not been clearly established (Vucetich, 1984; Patterson and Wood, 1982; Walton, 1997). *Neoreomys* Ameghino, 1887 is one of the most abundant extinct caviomorphs of the Miocene of Patagonia, and is recognized from the "Pinturan" (late Early Miocene; Kramarz, 2006) to the "Colloncuran" (Middle Miocene; Vucetich *et al*., 1993). *Neoreomys australis* Ameghino, 1887 is the only species of the genus recognized in the Santa Cruz Formation (Kramarz, 2006).

Eocardiids include small- to medium-sized caviomorphs, recognized from the Late Oligocene to the Middle Miocene (e.g. Ameghino, 1887; Scott, 1905; Wood and Patterson, 1959; Patterson and Wood, 1982; Vucetich, 1984; Kramarz, 2006; Pérez *et al*., 2010a, b) mainly in Patagonia, but have recently been recorded from San Juan, Argentina (López *et al*., 2011), Pampa Castillo and Curá Mallín, Chile (Flynn *et al*., 2002; Flynn *et al*., 2008), and Quebrada Honda, Bolivia (Croft, 2007).These rodents were traditionally related to the origin of Caviidae (cavies and maras) and Hydrochoeridae (the large capybaras) (e.g. Scott, 1905; Kraglievich, 1932; Patterson and Wood, 1982; Kramarz, 2006). However, recent phylogenetic studies (Pérez, 2010a, b; Pérez and Vucetich, 2011) of Cavioidea *sensu stricto* (*sensu* Patterson and Wood, 1982: 510) supported the paraphyly of "Eocardiidae" and, therefore, quotation marks are used for this assemblage of basal cavioids. The crown group of Cavioidea *s.s*. is formed by Caviidae + Hydrochoeridae, excluding the basal forms (i.e. "Eocardiidae"). According to Pérez (2010a) the second large diversification in the evolutionary history of cavioids *s.s*. occurred during the Santacrucian, represented by several Patagonian species of "Eocardiidae", such as *Eocardia montana* Ameghino, 1887, *E. excavata* Ameghino, 1894, *E. fissa* Ameghino, 1891, *Luantus toldensis* Kramarz, 2006, *Phanomys mixtus* Ameghino, 1887, *Ph. vetulus* Ameghino, 1891, *Schistomys erro* Ameghino, 1887, and *S. rollinsii* Scott, 1905 (Pérez, 2010a). *Eocardia fissa* is one of the most common caviomorph rodents recovered from the Santa Cruz Formation (Pérez, 2010a).

Octodontoids (not discussed in this chapter) constitute the most diverse clade of caviomorphs (Nowak, 1991). They were well represented in Patagonia during the Santacrucian (Ameghino, 1887; Scott, 1905), with six genera (i.e. *Sciamys* Ameghino, 1887, *Acaremys* Ameghino, 1887, *Spaniomys* Ameghino, 1887, *Stichomys* Ameghino, 1887, *Adelphomys* Ameghino, 1887, and *Acarechimys* Patterson, 1965) and more than 20 recognized species (Ameghino, 1887; Scott, 1905) that require detailed systematic revision. Available information indicates that Santacrucian octodontoids were small rodents with a body size apparently no larger than 1 kg (*Spaniomys riparius* Ameghino, 1887, 649 g; *Stichomys regularis* Ameghino, 1887, 492 g; Croft, 2000).

Chinchilloids (not treated in this chapter) include Dinomyidae, Neopiblemidae, and Chinchillidae (McKenna and Bell, 1997). The extinct *Perimys* Ameghino, 1887 (Neopiblemidae) is the only Neopiblemidae identified during the Santacrucian age, with several recognized species (Scott, 1905; Kramarz, 2002), which show a relatively wide range of body size (*Perimys* cf. *erutus* 585 g, *Perimys* sp. 326 g; Croft, 2000). Among Santacrucian chinchillids, nine species are included in the genera *Pliolagostomus* Ameghino, 1887 and *Prolagostomus* Ameghino, 1887, all smaller than the living *Lagostomus maximus* (*Prolagostomus oblicuidens* Scott, 1905, 2591 g; Croft, 2000).

15.3 Materials and methods

15.3.1 Materials

Institutional abbreviations Specimens of extinct caviomorphs studied here are housed in the Colección Nacional Ameghino of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-A), Buenos Aires, Argentina and the Museo Regional Provincial "Padre M. J. Molina" (MPM-PV), Rio Gallegos, Santa Cruz Province, Argentina.

Specimens of living caviomorphs examined are housed in the Museo de La Plata, La Plata, Argentina (MLP); Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Argentina (MMP); Museo Argentino de Ciencias

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Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Museu Nacional, Rio de Janeiro, Brazil (MN); Fundação Zoobotânica do Rio Grande do Sul, (FZB/RS); Museu de Ciências Naturais, Porto Alegre, Brazil (MCN), and Centro Nacional Patagónico, Puerto Madryn, Argentina (CENPAT).

We studied those Santacrucian caviomorphs that are known by associated and well-preserved cranial and postcranial remains. These include the cavioids *Eocardia fissa* ("Eocardiidae") and *Neoreomys australis* (Dasyproctidae), and the porcupine *Steiromys duplicatus* (Erethizontidae). Scott (1905) provided a mainly descriptive treatment of the species. Although chinchilloids and octodontoids are not analyzed in this study, they are noted where relevant.

The specimens of extinct caviomorphs studied herein are listed in Appendix 15.1. Fossil materials housed in MPM-PV were recovered between 2003 and 2011 by a joint team from the Museo de La Plata (Argentina) and Duke University (USA). All fossil specimens are from the Santa Cruz Formation (late Early Miocene, Santa Cruz Province, Argentina).

15.3.2 Methods

Body mass Body masses of the Santacrucian rodents analyzed here were estimated from allometric equations obtained by Biknevicius *et al*. (1993), based on the anteroposterior diameters of both the femur and humerus, and by Croft (2000), based on the length of the upper (M1) and lower (m1) first molars. For functional interpretations we use the body mass estimates obtained by applying the equations of Biknevicius *et al*. (1993), because they resulted in better estimators than the equations of Croft (2000), as explained below in Results. The body masses so obtained were averaged for subsequent analyses.

Feeding habits The identification of the areas of origin and insertion of the masticatory muscles in extinct species is based on muscle scars and fossae on the skull and the lower jaw, following the pattern observed by us and from the literature (Woods, 1972) in living caviomorphs, and information on other living mammals (Maynard Smith and Savage, 1959; Turnbull, 1970; Woods and Howland, 1979; Woods and Mackeen, 1989; Greaves, 1991; Samuels, 2009). Qualitative features that have been identified as functionally significant for interpreting the feeding habits of other rodents (e.g. Turnbull, 1970; Samuels, 2009) are also considered in the evaluation of the extinct species. Dental features and degree of hypsodonty are qualitatively evaluated in each case by comparison with the characteristic patterns of the extant related forms.

Locomotion Locomotor habits of *Steiromys duplicatus* were recently evaluated by Candela and Picasso (2008). Here we provide a synopsis of the main postcranial features that, according to these authors, are functionally significant for inferring the locomotor behavior of this species. Postcranial remains of *Neoreomys australis* are compared especially with those of the living cavioids *Dasyprocta* (Dasyproctidae) and *Agouti paca* (Agoutidae), and analyzed from a morphofunctional perspective. *Dasyprocta* was selected as it is a member of the same family in which *Neoreomys* is traditionally placed. Extensive comparisons were also made between *Neoreomys* and *Agouti paca* because of the postcranial resemblances between them. The main postcranial features functionally associated with different locomotor habits (including the capacity to climb, run, and leap) identified in caviomorphs and in other rodents by Elissamburu and Vizcaíno (2004), Samuels and Van Valkenburgh (2008), Candela and Picasso (2008), and Candela and Vizcaíno (2007) were used as a model to infer their functional significance in Santacrucian species. We especially discussed the muscular and associated osteological features that are relevant for functional interpretations. In this sense, the areas of articulation and muscular attachment were emphasized in our analysis. We mainly followed the myological nomenclature and system arrangement of McEvoy (1982) and García Esponda and Candela (2010). Terminology of the postcranial features of caviomorphs mainly follows Candela and Picasso (2008).

15.4 Results

15.4.1 Body mass

The results of the body mass estimations are shown in Table 15.1. At least in the case of one specimen of *Pediolagus salinicola* with known body mass, femoral and humeral measurements produced better estimates than molar lengths. Average body masses of the Santacrucian species, obtained from long bones, are 14.17 kg for *Steiromys duplicatus*, 2.83 kg for *Eocardia fissa*, and 7.12 kg for *Neoreomys australis*. Body masses obtained from equations based on molar lengths (Croft, 2000) are shown for comparative purposes.

15.4.2 Feeding habits

Results on feeding habits are preliminary because the analysis of masticatory apparatus in Santacrucian caviomorphs included here is in progress.

The masticatory apparatus of *Steiromys duplicatus* (Fig. 15.2) shows some differences from those of extant porcupines. The sagittal and temporal crests (origin of the main part of the temporal muscle; Woods, 1972) and the posterior zygomatic root (origin of the orbital part of the temporal muscle; see Fig. 15.2a) are more developed than in living porcupines, suggesting that the temporal muscle was better developed in this fossil form (see Turnbull, 1970; Samuels, 2009). The anterior part of the

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Table 15.1. *Body mass estimations of the studied specimens*

	Body mass estimates							
	Humerus	Femur	Mean	M1	m1	Mean	Body mass (kg)	Sources
Dasyproctidae								
Neoreomys australis	6.13±1.76 (2)	8.9±1.54 (5)	7.52	4.09±1.35 (15)	6.2±1.93 (7)	5.14		
Dasyprocta							1.3–4	a
Myoprocta							0.6–1.3	a
Agoutidae								
Agouti paca							7.5	b
"Eocardiidae"								
Eocardia fissa		2.838	2.838	0.8	1.33	1.06		
Caviidae								
*Pediolagus salinicola**	2.158	2.267		0.697	1.998		2	b
Dolichotis patagonum							8	c
Erethizontidae								
Steiromys duplicatus	16.27	12.07	14.17	5.72				d
Erethizon dorsatum							10–12	e
Coendou prehensilis							4.7	b
Chaetomys subspinosus							1.3	a
"*Sphiggurus*"							1.5–2.5	b

Note: Estimates based on anteroposterior diameters of humerus and femur (equations from Biknevicius *et al*., 1993) and first molar length (equations from Croft, 2000). a, Nowak, 1991; b, Redford and Eisenberg, 1992; c, Campos *et al*., 2001; d, Candela and Picasso, 2008; e, Miles *et al*., 1985.

* indicates known body mass of specimens. Species in bold face type indicate extinct genera analyzed in this chapter.

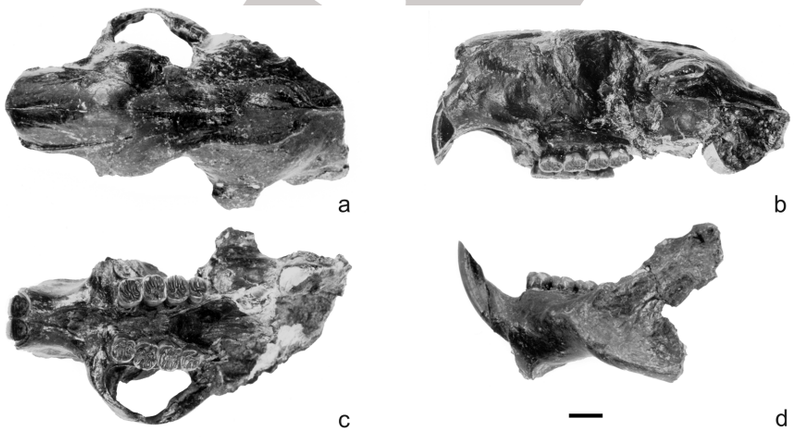

Fig. 15.2. *Steiromys duplicatus* MACN-A 10053–54; a–c, skull in dorsal (a), lateral (b), and ventral (c) views; d, right dentary in lateral view (reversed). Scale bar = 1 cm.

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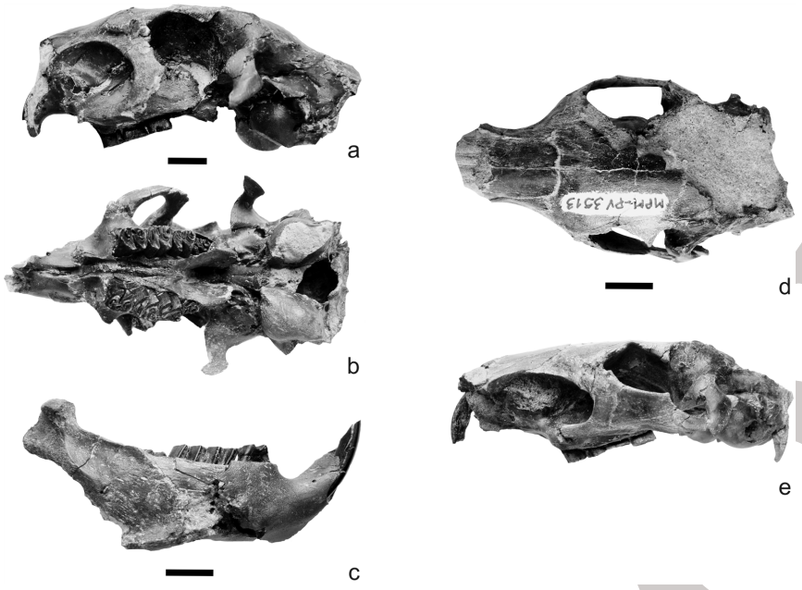

Fig. 15.3. *Neoreomys australis*. MPM-PV 3515, a–c, skull in lateral (a), and ventral (b) views, (c) right dentary in lateral view. MPM-PV 3513, d, e, skull in dorsal (d) and lateral (e) views. Scale bar = 1 cm.

medial masseter muscle also seems to have been more developed in *S. duplicatus* than in the extant species, as indicated by the larger rostral fossa of the zygomatic (*sensu* Candela, 2000) and deeper masseteric fossa of the mandible. The tuberosity on the ventral zygomatic root is very prominent, indicating a strong superficial masseter muscle, and the well-developed masseteric crest indicates also a strong lateral masseter muscle. The mandibular condyle (Fig. 15.2d) is relatively more dorsal with respect to the cheek teeth than in extant genera. In addition, the incisors in *S. duplicatus* (see Fig. 15.2b–d) are more robust, broader, and anteroposteriorly deeper, and more deeply implanted than those of extant porcupines (see Candela, 2000). Like living Neotropical species, the cheek teeth of *Steiromys duplicatus* are brachydont, but with thicker enamel, and the trend to early closure of the flexi (see Candela, 2000). The lower molars have five lophids (one more than those of *Coendou* spp.).

In *Neoreomys australis*, even in those more juvenile specimens, the rostral fossa (see Fig. 15.3a, b) is deeper than in *Dasyprocta*, a condition that reflects an enlargement of the area of the origin of the anterior part of the medial masseter (Samuels, 2009). The superficial masseter in *Neoreomys* is more developed than in *Dasyprocta*, as indicated by the wider ventral zygomatic root and more prominent masseteric tuberosity. On the mandible, the medial fossa (*sensu* Candela, 2000; see Fig. 15.3c), for the insertion of the posterior part of the medial masseter, is also markedly deeper than in *Dasyprocta*, indicating that this muscle was relatively larger. The coronoid process is much more prominent than in *Dasyprocta*, indicating a stronger temporal muscle. One of the more distinctive features in *Neoreomys* is the relatively larger size and higher crowns of the cheek teeth (see Figs. 15.3a, b, 15.6a, b, and 15.7a) compared with *Dasyprocta*. In addition, *Neoreomys* has noticeably larger incisors than *Dasyprocta*. Unlike *Dasyprocta* (with sub-parallel tooth rows), the divergent tooth rows in *Neoreomys* reflect a different modality of mastication, but more information is necessary to evaluate the significance of this feature.

Preliminary observations indicate that the incisors in *Eocardia fissa* are proportionately larger than in living caviids (see Fig. 15.4b, d). The mandibular configuration (with a different location and differentiation of masseteric and horizontal crests; Fig. 15.4d) reveals a different arrangement of the masticatory musculature compared with living caviids. The functional significance of these features has not been evaluated yet. Euhypsodonty is fully developed in Santacrucian eocardiids. In addition to hypsodonty, the cheek teeth of *Eocardia* resemble those of *Pediolagus* and *Dolichotis* in shape and differential wear of the enamel. Eocardiids and the chinchilloids *Perimys*, *Prolagostomus*, and *Pliolagostomus* represent the only euhypsodont rodents of the Santacrucian Age.

15.4.3 Locomotor behavior

Porcupines Recently, Candela and Picasso (2008) developed a functional analysis of the postcranium of the Santacrucian erethizontid *Steiromys duplicatu*s (see Fig. 15.5). As in living

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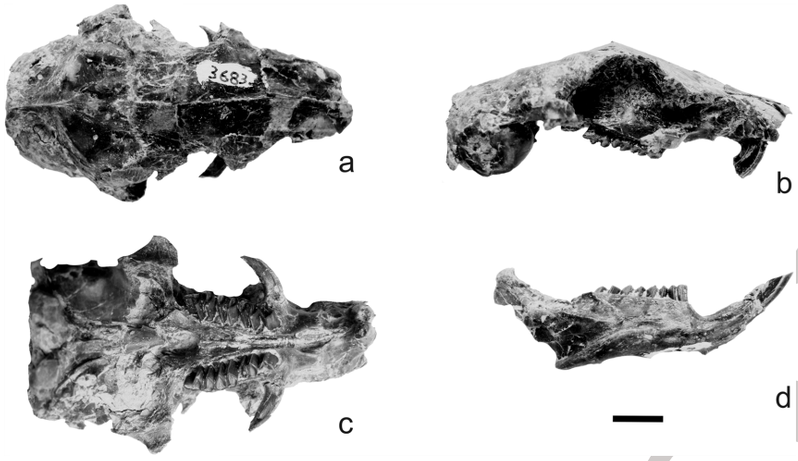

Fig. 15.4. *Eocardia fissa* MPM-PV 3683; a–c, skull in dorsal (a), lateral (b), and ventral (c) views; d, left dentary in lateral view (reversed). Scale bar = 1 cm.

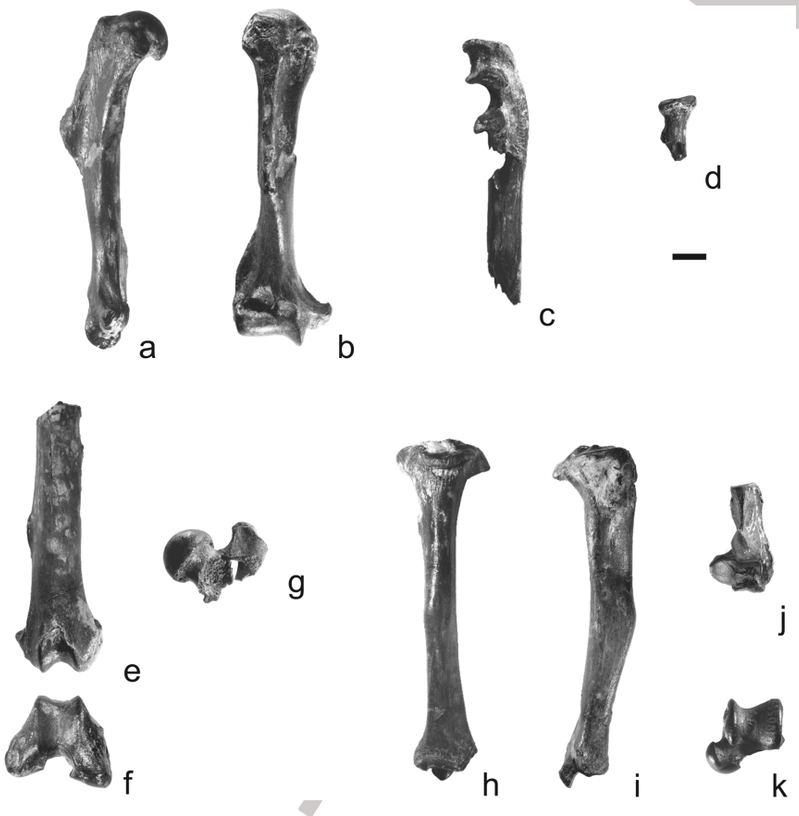

Fig. 15.5. *Steiromys duplicatus* MACN-A 10055–78; a, b, right humerus in medial and anterior views; c, left ulna in lateral view; d, proximal left radius in anterior view; e, f, distal right femur in anterior and distal views; g, proximal portion of the left femur in anterior view; h, i, left tibia in anterior and lateral views; j, right calcaneum in dorsal view; k, left astragalus in dorsal view. Scale bar = 1 cm.

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porcupines, several features of this species are compatible with the ability to climb. In the forelimb, the relatively low humeral tuberosities allow rotation at the gleno-humeral joint, a movement that is required for climbing. The prominent and relatively distally extended deltopectoral crest is indicative of a large *m. pectoralis major*, a powerful adductor that is particularly active during climbing (McEvoy, 1982). As in living porcupines and other arboreal mammals, the large and very protruding entepicondyle of *Steiromys duplicatus* indicates large *mm. pronator teres* and *flexor digitorum profundus*, both acting in climbing and grasping functions (McEvoy, 1982). Large *mm. brachioradialis* and *supinator*, as indicated by the prominent lateral epicondylar ridge, would have helped maintain stability at the radio-humeral joint (McEvoy, 1982; Candela and Picasso, 2008). The mechanical advantage of the *m. biceps brachii* is enhanced by the more distal attachment on the bicipital tuberosity, which reflects the powerful action of the flexor muscles (*mm. flexors biceps brachii* and *brachialis*) of the antebrachium during climbing at the beginning of the propulsive phase (McEvoy, 1982). As in living porcupines and other arboreal mammals (e.g. Szalay and Dagosto, 1980; Argot, 2001; Sargis, 2002), and differing from cursorial caviomorphs (see Candela and Picasso, 2008), the relatively shallow and non-perforated olecranon fossa of *S. duplicatus* reflects rotation at the elbow joint. Several features (concave radial notch, convex and very posteromedially extended ulnar facet of the radial head, globular capitulum) are indicative of a great range of pronation–supination movements. The wide trochlea–coronoid process contact area indicates an important function in supporting the body weight during the flexed and abducted forelimb on an arboreal substrate. A short but robust olecranon process of *S. duplicatus* indicates a strong insertion of the triceps brachii, which would act to catch new supports, aiding directional changes, during arboreal locomotion (Argot, 2002; Candela and Picasso, 2008). A short olecranon process also indicates a greater effective range of motion for the triceps muscles (Samuels and Van Valkenburgh, 2008).

In the hindlimb, the shape of the hip, knee, and cruroastragalar, calcaneoastragalar, and astragalonavicular joints in *Steiromys duplicatus* would have allowed lateral and rotational movements, although probably to a lesser degree than in extant porcupines (Candela and Picasso, 2008). The relatively large femoral head of *S. duplicatus* is compatible with a broad range in abduction of the femur, and the medially protruding lesser trochanter would have emphasized the abduction and outward rotation of the femur by the action of the iliopsoas complex during the recovery phase of climbing. As in extant porcupines, the relatively anteroposteriorly narrowed distal femoral epiphysis, combined with a wide femoral trochlea, may indicate a habitually flexed knee, which is characteristic of arboreal locomotion. This condition is less marked in *Steiromys duplicatus* than in Neotropical extant porcupines, indicating a lesser ability for abducting the femur in this species. The limited congruence between corresponding articular surfaces of the knee joint, as indicated by the shape of the femoral condyles and tibial platform with low tibial spines, facilitates rotational movements. The prominent and distally extended tibial crest indicates a powerful gracilis muscle, one of the main adductors of the hip and a powerful flexor of the hindlimb during climbing in extant porcupines (McEvoy, 1982). The posterior tibial muscle, an important invertor of the foot (McEvoy, 1982), would also have been well developed in *S. duplicatus*, as indicated by the great size of the medial tarsal bone (= first sesamoid; fig. 28 of Candela and Picasso, 2008), and by the relatively large and deep groove on the posteromedial side of the medial malleolus. This groove provides the path for the tendon of this muscle and for the *flexor digitorum tibialis*, an important plantar and digital flexor (McEvoy, 1982). The space between the tibia and fibula in *S. duplicatus* reveals a large origin area for the *m. flexor digitorum fibularis*, another important plantar and digital flexor, particularly active in forcing the claws into the substrate and in grasping branches during climbing (McEvoy, 1982). *Steiromys duplicatus* shows a relatively mobile cruroastragalar joint, as indicated by the morphology of the tibial articular surface for the astragalar trochlea. The distal tibial spine is poorly developed, thereby permitting lateral movements at this joint and facilitating the dorsiflexion, but possibly in a lesser degree than observed in *Coendou* (see Candela and Picasso, 2008). Plantar flexion is also facilitated by the posterior orientation of the posterior process of the tibia. According to Candela and Picasso (2008), the cruroastragalar joint of *S. duplicatus*, although mobile, would have been less so than in *Coendou*, because in the extinct species the lateral facet of the articular surface of the tibia is somewhat deeper, and the distinctive distal tibial spine would have acted as a stop, restricting dorsiflexion and lateral movements compared with *Coendou*. Lateral and rotational movements at the transverse tarsal joint in *S. duplicatus* are indicated by the large size, globular shape, and medial orientation of the astragalar head. This condition would have permitted inversion of the foot, so that the plantar surface turned medially during climbing. The importance of the medial region of the foot both for mobility and for supporting stress during climbing is revealed by the extensive contact between the astragalar head, the navicular, and the medial tarsal bone. The shape of the astragalar sustentacular facet of *S. duplicatus* is indicative of movements in a transverse direction, and the shape and orientation of the ectal facet of the calcaneum would have permitted lateral movements at the calcaneoastragalar joint. The slightly concave sustentacular facet suggests that these movements would have been less emphasized than in extant Neotropical species. As in

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extant porcupines, *S. duplicatus* has a relatively long tuber calcanei (in-lever arm) and a very short distal region of the calcaneum as well as a relatively short metatarsal (out-lever arm). This condition is more efficient in generating greater power but not speed, providing great effective force during climbing (see Candela and Picasso, 2008).

Among the most specialized features for grasping and foot inversion in living porcupines are the well-developed medial tarsal bone (= first sesamoid; see fig. 22 of Candela and Picasso, 2008), the hypertrophied medial sesamoid (more developed in *Coendou*), the medially oriented metatarsal I, and very curved claws, which reach their extreme development in *Coendou* (Jones, 1953; Grand and Eisenberg, 1982). In *Coendou*, the hallux is reduced and incorporated into the preaxial pad and the medial sesamoid is very large and particularly active during pedal grasping (Jones, 1953). The foot of *Erethizon dorsatum*, bearing a well-developed hallux and a smaller medial sesamoid, has not achieved the degree of specialization of *Coendou*. As in *E. dorsatum*, in *Steiromys duplicatus* the hallux is well developed, the medial sesamoid is smaller than in *Coendou*, the metatarsal I is not as medially oriented with respect to the remaining metatarsals as in *Coendou*, and the claws are less robust and deep than in the latter (fig. 22 of Candela and Picasso, 2008).

Dasyproctidae Recently, postcranial features of *Neoreomys australis* were identified as functionally related to parasagittal movements, compatible with cursorial habits (Candela and Vizcaíno, 2007). Most features of *N. australis* (Figs. 15.6 and 15.7) are shared with those of living *Agouti paca*. Proportions and relative size of all examined elements are more similar to those of *Agouti paca* than of *Dasyprocta* spp. Osteological features indicate that the muscles of *Neoreomys australis* were comparatively larger than in *Dasyprocta* spp. Humeral tuberosities of *N. australis*, especially the greater tuberosity, are higher than the humeral head, restricting the mobility of the glenohumeral joint, a condition shared with other cavioids (see Candela and Picasso, 2008). The deltopectoral crest, which provides the area of insertion for pectoral and deltoid muscles (see García Esponda and Candela, 2010), is more distally extended than in *Dasyprocta*, a condition similar to that of *Agouti paca*. As in the latter, the entepicondyle, which provides the origin for the flexor muscles of the antebrachium and manus, is more robust than in *Dasyprocta*, suggesting a large pronator teres, which stabilizes the humeroradial joint and supports the weight during locomotion. The reduction of the entepicondyle and the related flexor musculature (Jenkins, 1973) in *Dasyprocta* seem to be cursorial specializations of this more genus. As in *Agouti paca*, the lateral epicondylar ridge is more raised than in *Dasyprocta*. As in the latter, *Agouti*, *Dolichotis*, *Cavia*, and *Hydrochoerus*, the olecranal fossa is perforated in *Neoreomys australis*. This feature would facilitate anteroposterior movements, allowing the olecranal process to pass through the fossa during complete extension. The elbow joint of *N. australis*, which is relatively wider than that of *Dasyprocta*, has several features indicative of a preponderance of parasagittal movements. The trochlea is deep, although to a lesser degree than in *Dasyprocta*, a condition that increases the articular surface in a proximodistal direction (Candela and Picasso, 2008). As in *Agouti paca* and *Dasyprocta*, *N. australis* has a very distinctive medial trochlear keel, extended flanges, and a markedly developed capitular tail. These features would be effective for resisting mediolateral forces at the elbow, maximizing the correspondence of articular surfaces and stability at this joint. The radial head, which as in other cavioids (see Candela and Picasso, 2008) is anterior with respect to the ulna, is subrectangular (more laterally extended than in *Dasyprocta*), with a flattened and posteriorly located ulnar facet. The capitular eminence is well developed (resembling *Agouti paca*), probably acting in the stabilization of the joint. This configuration restricts movements at the elbow joint and increases stability during flexion/extension. The extended radial head would be more efficient in bearing loads at the humeroradial articulation during the propulsive phase of locomotion. As in *Dasyprocta* and *A. paca*, the greater trochanter of the femur projects farther proximally than the femoral head, which increases the mechanical advantage of the gluteal muscles (Maynard Smith and Savage, 1956). As in *Dasyprocta* and other cavioids, the lesser trochanter is posteriorly located. This position would indicate a more anteroposterior orientation of the fibers of the iliopsoas complex, facilitating parasagittal movements (Candela and Picasso, 2008). The distal femoral epiphysis is relatively deep. A deep knee, with an anteriorly projected tibial tuberosity (a feature less marked in *Neoreomys* than in *Dasyprocta*) increases the mechanical advantage of the quadriceps femoris, making it more powerful for flexion of the hip and extension of the knee. These conditions are consistent with efficient parasagittal propulsion during terrestrial locomotion. Like *Dasyprocta* and *Agouti paca*, *N. australis* has a relatively congruent knee articulation, which enhances stability, thereby restricting rotation of the tibia. As in *A. paca*, the tibia of *N. australis* is relatively shorter than that of *Dasyprocta*. The distally extended tibial crest of *N. australis* reflects an increased mechanical advantage of the hamstring muscles which are required for powerful extension of the hip at the beginning of propulsion and for flexion of the knee during the recovery stroke (Maynard Smith and Savage, 1956; Elftman, 1929). Features of the cruroastragalar joint of *N. australis* indicate restricted movements, because the tibial articular surface possesses a deep and concave lateral facet. The anteriorly projecting

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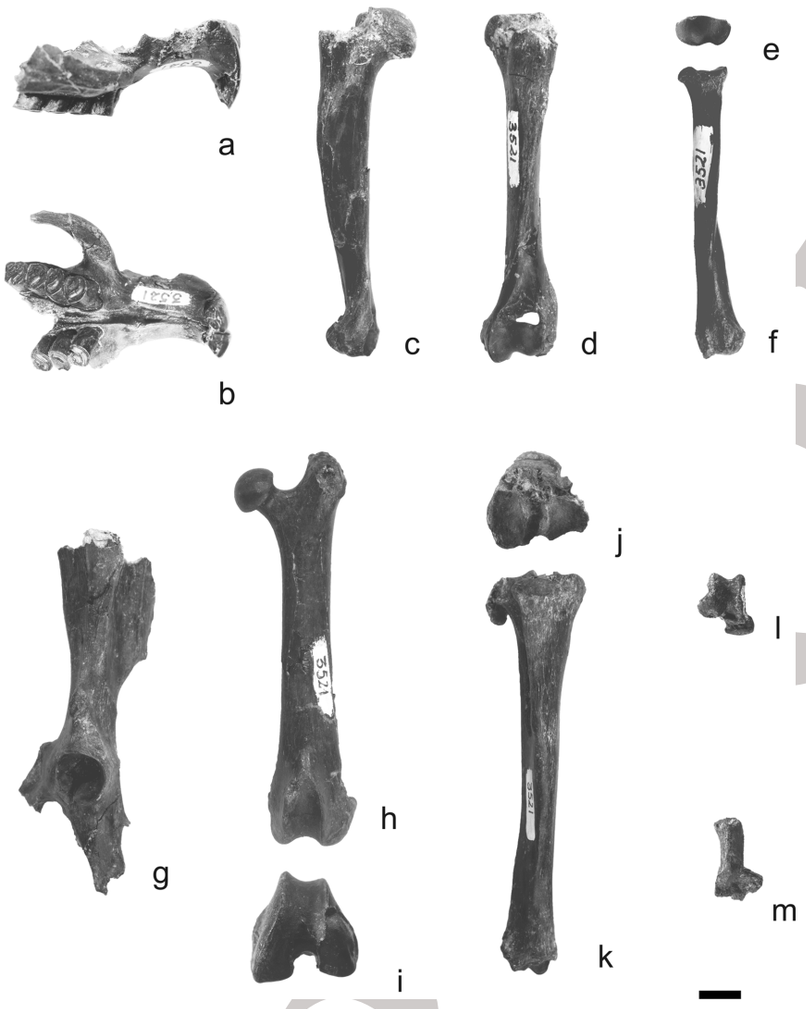

Fig. 15.6. *Neoreomys australis* MPM-PV 3521; a, b, cranial fragment in lateral and ventral views; c, d, left humerus in lateral and anterior views; e, f, left radius in proximal and anterior views; g, left pelvis in lateral view; h, i, left femur in anterior and distal views; j, k, right tibia in proximal and anterior views; MPM-PV 3517; l, right astragalus in dorsal view; m, calcaneum in dorsal view. Scale bar = 1 cm.

posterior process and the prominent anterior distal tibial spine act as stops to the movements at the upper ankle joint. As in *Dasyprocta*, *Agouti*, and caviids (see Candela and Picasso, 2008), the astragalar head in *N. australis* is oriented relatively parallel to the parasagittal plane, a condition that restricts flexion–extension movements. As in other cavioids, the distal portion of the calcaneum is very elongated, a condition that increases speed at the expense of force compared with arboreal forms (see Candela and Picasso, 2008). The shape and relative size of remaining elements of the feet are very similar to those of *Agouti paca* (e.g. the plantar process of the navicular is well developed but to a lesser degree than in *Dasyprocta*; the preserved facet for metatarsal I on metatarsal II is more developed than in *Dasyprocta*; metatarsals II–IV are more robust and relatively shorter than in *Dasyprocta*, even more than in *A. paca*).

"Eocardiidae" Forelimb features in *Eocardia fissa* available for this study are represented only by the proximal end of the ulna, for which the articular region is preserved. Even so, it is sufficiently preserved to allow the recognition of elbow joint features that, as in living cavioids, restrict mobility at this joint and increase stability of the joint during flexion and extension (see Candela and Picasso, 2008). In *E. fissa* the coronoid process of the ulna is comparatively narrow with respect to the radial notch, reflecting a narrow anterior contact with the humeral trochlea, as

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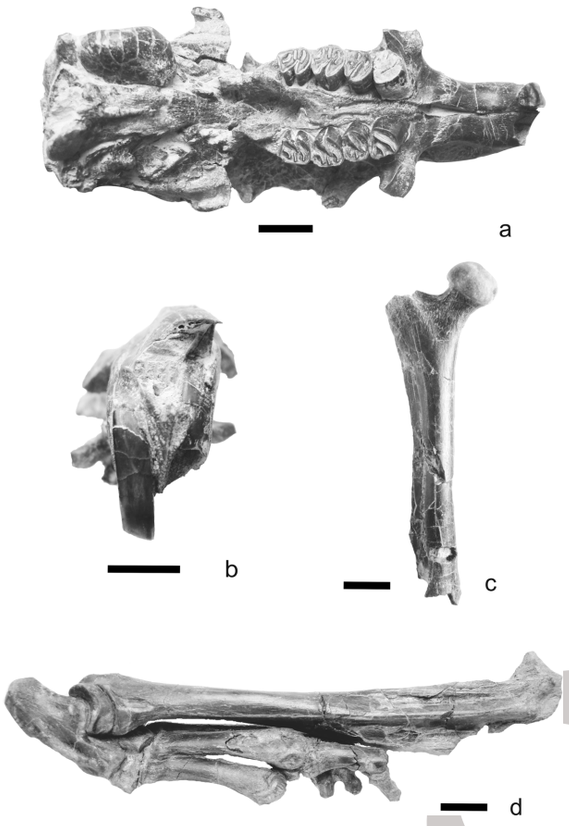

Fig. 15.7. *Neoreomys australis* MPM–PV 4342; a, b, skull in ventral and anterior views, c; right femur in anterior view; d, right tibia and articulated foot in lateral view. Scale bar = 1 cm.

occurs in living caviids (see Candela and Picasso, 2008). This condition indicates that the trochlea–coronoid process contact was anteriorly replaced by the trochlea–radial head contact. The relatively wide radial notch reflects a relatively wide radial head, which, as in living cavioids, was located anteriorly with respect to the ulna. As noted by Scott (1905), this condition prevented any rotational movement at the elbow joint. As in *Dolichotis* or *Cavia* (see fig. 8 of Candela and Picasso, 2008), the radial notch in *Eocardia fissa* is represented by two distinctive articular facets, one anterolaterally located, flattened, and subcircular, and the other extended medially towards the reduced coronoid process. This conformation limits radial supination and increases stability during flexion/extension (Candela and Picasso, 2008). According to Scott (1905: 467), in *Eocardia* there is much more disparity between the lengths of the fore- and hindlimbs than in any other member of the clade. We are unable to corroborate this information, but taking into account the measurements provided by Scott (1905), we note that *Eocardia* possessed relatively longer hindlimbs than those of *Dolichotis*. *Pediolagus* seems to have intermediate limb lengths, but more similar to that of *Dolichotis*. In addition, as was pointed out by Scott (1905: 470–471), *Eocardia* does not exhibit the elongation of the radius/ulna and tibia/fibula present in *Dolichotis*, instead having proportions more similar to those of *Cavia*. The remaining features of the hindlimbs in *Eocardia fissa* are compatible with emphasized parasagittal movements and stabilized joints. The portion preserved of the gluteal dorsal fossa of the ilium (Fig. 15.8) is deeper and wider than that of the living *Dasyprocta* and *Cavia*, being similar to that of

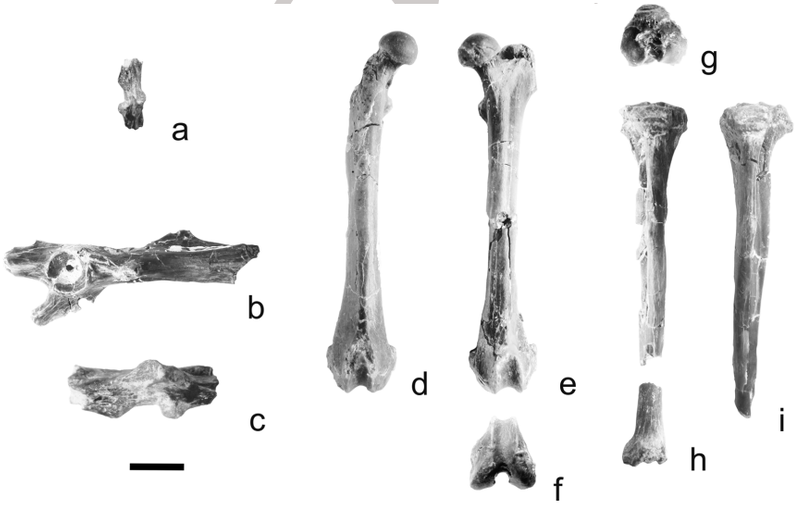

Fig. 15.8. *Eocardia fissa* MPM-PV 3683; a, right proximal fragment of the ulna; b, c, right and left pelvis in lateral view; d, right femur in anterior view; e, f, left femur in anterior and distal views; g, h, right tibia in proximal and anterior views; i, left tibia in anterior view. Scale bar = 1 cm.

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Pediolagus salinicola. This condition indicates that the medial gluteus muscle was relatively well developed, in agreement with an improved extension of the hip joint. As in *Pediolagus salinicola*, the tuberosity of the pelvis for the origin of *m. rectus femoris* is prominent, forming a robust protuberance, which is more developed than in the living cavies and *Dasyprocta*. This is in agreement with a strong development of this muscle, which acts as a flexor of the hip and extensor of the knee (García Esponda and Candela, 2010). A rapid extension of the knee is required in species with agile movements (e.g. Szalay and Sargis, 2001; Abello and Candela, 2010). A deep acetabulum limited by raised margins acts to partially restrict rotational movements in living caviids (Candela and Picasso, 2008; García Esponda and Candela, 2010). This configuration provides a relatively elevated congruence at the hip joint necessary to stabilize flexion/extension movements and accentuated parasagittal movements of the femur during locomotion. In the available sample, the degree of proximal extension of the greater trochanter of the femur is unknown, because the base of this structure is partially broken. However, the preserved portion of this trochanter (robust and relatively wide) indicates an extensive insertion area for the deep and medial gluteals, compatible with a powerful extension of the thigh during the propulsive phase of locomotion, a feature typical of cursorial species (e.g. Maynard Smith and Savage, 1956; Candela and Picasso, 2008; Salton and Sargis, 2009). The lesser trochanter is relatively more developed than in examined living cavies and it is caudally located, as in other cursorial caviomorphs (Candela and Picasso, 2008). This condition would improve the function of *m. iliopsoas* as a protractor, rather than as a rotator of the femur (Candela and Picasso, 2008; Salton and Sargis, 2009).

The distal end of the femur and proximal end of the tibia compose a deep knee. As in living caviids, this is characterized by a long and relatively narrow femoral trochlea, delimited by sharp crests, and a cranially projected tibial tuberosity. These features increase the mechanical advantage of *m. quadriceps femoris* in the extension of the knee (Fostowicz-Frelik, 2007; Candela and Picasso, 2008; Salton and Sargis, 2009; García Esponda and Candela, 2010). As in living caviids, the knee joint has prominent tibial spines and concave tibial condyles, which increase the congruence of corresponding articular facets at this joint, restricting mobility and rotation of the tibia. The lateral fossa of the tibia, from which the *m. tibialis cranialis* arises, is deeper than in living cavies and in *Dasyprocta*, being more similar to that of *Pediolagus* and *Dolichotis*. This muscle dorsiflexes the ankle joint and inverts the foot. It is possible that, as was interpreted for *Dasyprocta* (García Esponda and Candela, 2010), the *m. tibialis cranialis* in *Eocardia* acted principally as an extensor rather than as an inverter of the pes.

According to Scott (1905), the tibia is only slightly longer than the femur. In agreement with these data, the comparison of equivalent portions of the tibial shafts of *E. fissa* and *Pediolagus salinicola* indicates that this bone in the extinct species was somewhat longer than the femur but not to the extent observed in living species. Thus, although somewhat longer than the femur, the tibia of *E. fissa* is not as elongated as in *Dolichotis* and *Pediolagus*. Among the cavioids examined here, elongation of the tibia, a feature functionally associated with cursorial or saltatorial habits (Gambaryan, 1974), was only observed in the extreme cursors *Dasyprocta*, *Pediolagus*, and *Dolicthotis* (García Esponda and Candela, 2010). As in living cavioids (see Candela and Picasso, 2008), the distal tibial articular surface possesses deep and concave lateral and medial facets, which indicate restricted lateral movements at the upper ankle joint. The distinctive anterior distal tibial spine would have offered a stop to dorsiflexion and lateral movements at this joint. These features indicate that the upper ankle joint in *E. fissa* was relatively stable, as in living cavioids. The shape and relative size of foot elements (e.g. configuration of the cuboidal facet of the calcaneum, well-developed plantar process of the navicular, presence of three functional metatarsals, rudimentary facet on the metatarsal IV for metatarsal V) indicate that the foot was digitigrade (see Scott, 1905), as is the tarsus of living caviids (A. M. Candela *et al*., unpublished data). All of these features are compatible with emphasized parasagittal movements. In summary, the postcranial morphology of *Eocardia*, characterized by marked joint stability, a prominent femoral tubercle, and a deep knee, among other features, constitutes an arrangement better suited for flexion–extension movements. Stabilized joints are in agreement with the necessary stability required to run or leap. These features are well suited for a cursorial and agile mode of locomotion. As in living *Dolichotis* and *Pediolagus*, leaping could have been a part of the locomotor behavior of *Eocardia fissa*, which likely had a locomotor pattern similar to that of the extant *Pediolagus salinicola* (see Discussion).

15.5 Discussion

According to our results, *Steiromys duplicatus*, with body mass of nearly 14 kg, was larger than extant Neotropical porcupines. *Coendou prehensilis*, the largest species of this genus, weighs about 4.5 to 4.9 kg, while "*Sphiggurus*" ranges from 1.5 to 2.5 kg (see Table 15.1). The only living New World porcupine that surpasses the body mass of *Steiromys duplicatus* is the Holartic *Erethizon dorsatum*, typically 10 to 12 kg (Miles *et al*., 1985), but occasionally reaching 18 kg (Woods, 1973).

Estimated body mass for *Eocardia fissa* is similar to that of the caviid *Pediolagus salinicola* ("conejo de los palos").

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The latter, with an average body weight of 1.9 to 2.1 kg and a maximum of 2.7 kg, is the smallest living Dolichotinae, but it is larger than any living Caviinae (guinea pig; cavies). *Eocardia fissa* was thus larger than the largest living cavy *Cavia aperea* (0.5 to 1.5 kg; average weight 460 g). The "conejo de los palos" can be a suitable analog for interpreting the paleobiology of *E. fissa*. Average estimated body mass of *Neoreomys australis* is closer to the cursorial rodent *Agouti paca* (6 to 12 kg; average weight 7.5 kg; see Table 15.1) than to the species of *Dasyprocta* (1.3 to 4 kg). *Neoreomys australis* represents the largest Santacrucian cavioid and one of the largest Miocene caviomorphs from Patagonia.

In summary, our results indicate that the caviomorphs from the Santa Cruz Formation examined here exhibit a range of body masses between approximately 1 kg and 14 kg. Small-, medium- and relatively large-sized caviomorphs are recorded from the Santacrucian, with the smallest represented by octodontoids, the largest by the paca-like *Neoreomys australis* and the porcupine *Steiromys duplicatus*, and the medium-sized forms by the eocardiids.

The few studies on the ecology of Neotropical porcupines have noted that their feeding strategy is based mainly on fruits, seeds, buds, and soft leaves (Charles-Dominique *et al*., 1981; Emmons and Feer, 1997). The semi-arboreal Holartic *Erethizon dorsatum*, mainly inhabiting temperate woodlands, consumes mostly harder food than Neotropical species, such as bark, coniferous leaves, and seeds (Roze, 1989). Osteological features of *Steiromys duplicatus* indicate that the masticatory muscles were stronger than in living Neotropical species. As was demonstrated in other rodents, a more massive skull could serve to accommodate stresses resulting from mastication and to support larger masticatory muscles (Samuels, 2009: 881). This increase of the mass of the adductor muscles in *S. duplicatus* may result from scaling effects related to its larger size with respect to the living species. The relatively anteroposteriorly thick and more deeply implanted incisors in *S. duplicatus* probably better resisted forces resulting from biting harder foods than in Neotropical porcupines (Samuels, 2009). Pentalophodont lower molars of *S. duplicatus* provided an increased number of surfaces available to cut or grind than in living porcupines, which would have favored the grinding action of the occlusal surfaces (Evans *et al*., 2007; Samuels, 2009).

Consequently, *Steiromys duplicatus* presents features that indicate a diet of harder and more abrasive food items than those consumed by living Neotropical species. Its diet was probably more similar to that of *Erethizon dorsatum*, perhaps a specialization related to living in more open areas than in rainforest (see Section 15.6: Paleoenvironments).

The same situation is found in the dasyproctid *Neoreomys australis*, which exhibits features (e.g. higher crowned molars and relatively larger cheek teeth and incisors) that indicate that this species was capable of consuming harder food items than those consumed by living species of *Dasyprocta*. The feeding strategy of *Dasyprocta* spp. is based mainly on fruits, seeds, buds, and soft leaves (Charles-Dominique *et al*., 1981; Emmons and Feer, 1997).

Eocardia fissa, with euhypsodont and heart-shaped cheek teeth, similar to those of *Pediolagus salinicola* and *Dolichotis patagonum*, may have favored a diet similar to these extant rodents, both of which consume a relatively high proportion of grasses and herbs, as well as leaves of shrubs and trees (Campos *et al*., 2001; Chillo, 2007). A recent study (Chillo, 2007) indicated that *Pediolagus salinicola* and *Dolichotis patagonum* consume the same food items (leaves of trees, shrubs, and grasses), but in different proportions (*P. salinicola* prefers leaves of trees, herbs, and grasses while *D. patagonum* prefers grasses). Features of the masticatory apparatus of *E. fissa* are compatible with the ability to consume these food items, and suggest a relatively wide food spectrum, including abrasive foods.

Among Santacrucian caviomorphs different locomotor behaviors were represented, as indicated by the presence of semi-arboreal, relatively large cursorial, and smaller and more agile cursorial forms. Although exhibiting diverse forms of locomotion, none of them achieved the degree of specialization seen in living related taxa. *Steiromys* did not achieve a highly arboreal lifestyle like that of Neotropical porcupines (Candela and Picasso, 2008). *Neoreomys australis* would not have had the capacity to move with the remarkable speed and agility achieved by *Dasyprocta* (Nowak, 1991). In fact, at least some features of *Dasyprocta* may have originated in association with the development of a highly cursorial lifestyle (García Esponda and Candela, 2010). On the other hand, body size and most of the postcranial features of *Neoreomys australis* (e.g. general limb proportions) are more similar to those of *Agouti paca* than to *Dasyprocta*. *Agouti paca*, which inhabits mainly tropical forests, is a cursorial rodent with voluminous body that can run and is capable of swimming with agility (Mondolfi, 1972). It is thus plausible that *Neoreomys* had swimming abilities.

Estimated body mass and functional analysis of postcranial features of *Eocardia fissa* suggest that this species would have had a locomotor behavior similar to that of living *Pediolagus salinicola*. Like the mara, *Dolichotis patagonum*, the smaller *P. salinicola* is characterized by cursorial habits and the ability to leap and run with remarkable speed and agility (Nowak, 1991). Most of the osteological traits observed in *Eocardia fissa* are compatible with such habits, although to a lesser degree than in extant forms. Thus for example, *E. fissa* does not exhibit the marked elongation of the distal limb elements of *Pediolagus* and *Dolichotis*.

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Santacrucian caviomorphs indicate ecological niche partitioning: *Steiromys* would have been semi-arboreal and adapted to consume harder food items than those eaten by extant Neotropical species; *Neoreomys* a relatively large cursorial rodent with some ability to swim, and feeding on moderately more abrasive food than extant species; and *Eocardia* an agile cursorial and probably a "mixed feeder" (forbes and grasses) capable of consuming relatively abrasive food items.

15.6 Paleoenvironments

As discussed above, characteristics of *Eocardia fissa* resembled those of living *Pediolagus salinicola*, an agile cursorial rodent adapted to eating relatively abrasive food. *Pediolagus* inhabits the arid and semi-arid bushland and relatively open forested areas of the Chaqueña Province (*sensu* Cabrera and Willink, 1980), and regions with thorn scrubs, characterized by warm climatic conditions and marked seasonality. Relatively open areas, with notable variation in rainfall, may have been the appropriate environment inhabited by *Eocardia fissa*. On the other hand, characteristics of the relatively large porcupine *Steiromys duplicatus* indicate that this species was not as highly arboreal as living Neotropical species, but rather semi-arboreal, resembling the living Holartic *Erethizon dorsatum*. The habitat occupied by *Steiromys duplicatus* was possibly more open than that inhabited by *Coendou*. *Steiromys duplicatus* indicates the presence of forested environments with certain variation in rainfall, unlike the evergreen rainforests inhabited by highly arboreal porcupines. The cursorial paca-like *Neoreomys australis* suggests the presence of relatively warm forested areas, probably associated with water bodies.

Taken together, the composition and paleobiological characteristics of Santacrucian caviomorphs denote the presence of mixed woodland habitats, with probable seasonality in rainfall patterns, similar to the Brazilian Cerrado biome. This is a vast tropical semideciduous savanna composed of a mosaic of subunits, ranging from open grassland to dry forest, with gallery forest, composed of evergreen trees usually with a sparse understory (Eiten, 1972, 1974; Fernandes and Bezerra, 1990). The Cerrado biome includes significant variation in vegetation types, forming a gradient from completely open "cerrado" ("campo limpo," clean field), dominated by grasses and low bushes with a total absence of arboreal cover, to the "cerrado *s.s.*" and the "cerradão," a closed canopy forest characterized by a higher density of trees with a semi-open canopy. The intermediate forms include the dirty field (the "campo sujo") and the "campo cerrado" (savanna), having an increasing density of trees (e.g. Eiten, 1972, 1974; Ferandes and Bezerra, 1990). The climate is hot, semi-humid, with pronounced seasonality marked by a dry winter season (CODEPLAN, 1976). The wide variability of habitats in the different types of "cerrado" currently supports an enormous diversity of plants and animals species. Redford and Fonseca (1986) noted that 50% of cerrado species are characterized as wide-ranging (found in both forest and savanna biomes), such as armadillos, giant anteater *Myrmecophaga tridactyla*, and the canid *Chrysocyon brachyurus*, which occur in both open and forested areas. For these species, gallery forests may be particularly important during the dry season, as well as in years of decreased rainfall (Redford and Fonseca, 1986). Cerrado also includes several forest-adapted species, such as monkeys and porcupines, and species associated with permanent water bodies, such as *Chironectes minimus*, *Pteronura brasiliensis*, *Lontra longicaudis*, *Hydrochoerus hydrochaeris*, and *Agouti paca* (Redford and Fonseca, 1986; Cáceres *et al*., 2008). The environment in which the numerous Santacrucian species lived may have been similar to the heterogeneous and diverse landscape of the Cerrado biome. A complex mosaic of open and closed habitats would have been favorable to the coexistence of Santacrucian species with different lifestyles: forest-adapted species, such as primates and porcupines; species associated with water bodies, such as paca-like rodents, and wide-ranging species, which probably lived in both forest and savanna biomes, such as certain armadillos and rodents like "conejo de los palos." Information provided by Santacrucian caviomorphs, in association with other sources of information (e.g. paleoclimate, paleobotanic evidence), will facilitate interpretation of their paleohabitats.

15.7 Conclusions

1. Santacrucian caviomorphs showed a range of body mass, as represented by small- to relatively large-sized living caviomorphs.
2. The range of sizes and morphological disparity in the masticatory apparatus of Santacrucian caviomorphs (including different degree of crown height, development of masticatory muscles) suggest differences in the degree of food selection. The porcupine *Steiromys duplicatus* and the dasyproctid *Neoreomys australis* probably had diets of harder and more abrasive food items than those consumed by related living Neotropical species. The eocardiid *Eocardia fissa* consumed a wide variety of items, including relatively coarse foods.
3. Santacrucian rodents had different locomotor behaviors and use of substrates. *Steiromys duplicatus* was a semi-arboreal form, which did not reach the degree of specialization seen in highly arboreal Neotropical species. *Eocardia fissa* was probably an agile cursorial species, similar to the living *Pediolagus salinicola* ("conejo de los palos"). *Neoreomys australis* was a

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cursorial rodent, more similar to the living *Agouti paca* (Agoutidae) than to living species of *Dasyprocta*.

4. These species could have inhabited different areas or microhabitats within a mosaic environment comparable to the Brazilian Cerrado. Santacrucian caviomorphs developed differential resource utilization patterns with marked differentiation of their ecological niches.

ACKNOWLEDGMENTS

We thank C. García Esponda for comments and suggestions that improved the manuscript, and D. Flores (MACN), U. Pardiñas (CENPAT), D. Romero (MMP), and A. Kramarz (MACN), for facilitating access to specimens under their care. We extend special thanks to S. F. Vizcaíno, R. F. Kay, and M. S. Bargo for providing the new specimens collected during Museo de La Plata/Duke University expeditions and for inviting us to take part in this book. We thank A. Gainza for her help with the translation; D. Voglino for the illustrations and information on Cerrado biome; Michelle Arnal for providing information on Santacrucian Octodontoidea. We especially appreciate the editorial support and thank G. De Iuliis and the reviewers X. J. Samuels and M. G. Vucetich for their helpful comments and suggestions that substantially improved the manuscript. This is a contribution to the projects PICT 0143 to Sergio F. Vizcaíno, and NSF 0851272, and 0824546 to Richard F. Kay.

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Appendix 15.1 List of examined specimens of extinct caviomorphs

Specimens of extinct caviomorphs are from the Santa Cruz Formation (Santa Cruz Province, Argentina). See Vizcaíno *et al*. (Chapter 1: Figs. 1.1 and 1.2 and Appendix 1.1) for information on the localities, and Matheos and Raigemborn (Chapter 4: Figs. 4.3 and 4.4) for stratigraphy.

Eocardia fissa

MPM-PV 3683, almost complete skull, left and right dentaries, left and right pelvis, left and right femora and tibiae, proximal portion of right ulna. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 7; Puesto Estancia La Costa, Santa Cruz Province.

Steiromys duplicatus

MACN-A 10053–54, skull and right dentary. Horizon and locality: Santa Cruz Formation; Corriguen Kaik, Santa Cruz Province. MACN-A 10055–78, maxillary fragment with left P4–M3 and right M1–M2, left dentary with p4–m3, right humerus, distal portion of left humerus, left ulna, proximal portion of left radius, right femur, proximal and distal portions of the left femur, left tibia, distal and proximal portions of right tibia, left astragalus, and portions of the vertebral column. Horizon and locality: Santa Cruz Formation; Corriguen Kaik, Santa Cruz Province. MPM-PV 4273, skull and right mandible. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous level 5.3; Puesto Estancia La Costa, Santa Cruz Province.

Steiromys detentus

MPM-PV 4358, right dentary with dp4–m2. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4271, portion of skull with incisors and right P4 and left P4–M2. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province.

Neoreomys australis

MPM-PV 3513, almost complete skull, atlas, axis and proximal portion of left femur. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3514, incomplete skull and left femur. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 3515, almost complete skull and right dentary. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3516, proximal portion and shaft of right femur. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3517, partial left dentary, right astragalus, and right calcaneum. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3518, rostrum with incisors, pelvis fragment, proximal fragments of left femur and left tibia. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3519, almost complete skull, left and right dentaries, distal portions of left tibia and fibula, and portion of right scapula. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3520, portion of right dentary, and right humerus. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3521, fragment of skull, left femur and tibia, incomplete pelvis, right humerus, radius and incomplete scapula, two vertebrae. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3522, almost complete skull and left femur. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3523, incomplete skull, proximal portion of left femur. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Anfiteatro, Santa Cruz Province. MPM-PV 3674, skull fragment, right dentary fragment, head of left femur, distal portions of left and right tibia. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 3676, incomplete skull. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4339, almost complete skull. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 7; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4340, incomplete skull, left dentary, proximal portion of left femur and associated portion of pelvis, right portion of pelvis, distal portion of right tibia. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member,

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Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4341, almost complete skull, left and right femora and tibiae, right portion of pelvis, one vertebra. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4342, almost complete skull, left and right dentaries, right femur, tibia, and almost complete foot. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4343, almost complete skull and three vertebrae. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4344, left dentary. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3; Puesto Estancia La Costa, Santa Cruz Province. MPM-PV 4345, incomplete skull. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member; Campo Barranca, Santa Cruz Province.

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